A NEW QUASISOCIAL ANELOSIMUS SPIDER (ARANEAE, THERIDIIDAE) FROM PARAGUAY

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INTRODUCTION

The genus *Anelosimus* was last revised by Levi (1956, 1963). Since these revisions, considerable attention has been given to the study of the social behavior of spiders (Kullmann, 1968, 1972; Shear, 1970), and especially to the social behavior of species of *Anelosimus* (Brach, 1977). One species, *Anelosimus eximius*, constructs communal webs that encompass many cubic meters (Simon, 1891), and is considered by Wilson (1971) to have reached the level of quasisociality. We now describe and provide observations on a new quasisocial *Anelosimus* from southern South America.

Anelosimus lorenzo Levi, new species Figures 1–4

Holotype. Male holotype and numerous female paratypes, all in poor condition, having once been dry, San Lorenzo, Paraguay, collection 25 July, 1976, (H. Fowler) in the Museum of Comparative Zoology.

Diagnosis. The male of this species differs from *Anelosimus rupununi* Levi by the shape of the conductor in the palpus. No differences are known in females.

Description. Female. Carapace brown with wide darker median longitudinal band. Sternum, legs brown. Dorsum of abdomen white, with a line of black patches. Sides dark. Venter black with white spots toward sides. White behind and above spinnerets. Anterior median eyes subequal in size, larger than posteriors which are 0.7 diameters of anteriors. Anterior median eyes 1.8 diameters apart, a third of their diameter from laterals. Posterior median eyes 2 diameters apart, 1.5

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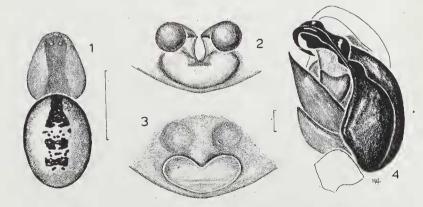
diameters from laterals. The height of the clypeus equals 3 diameters of the anterior median eyes. The abdomen is suboval, longer than wide, and high. Total length, 2.3 mm. Carapace 1.1 mm long, 0.9 mm wide. First femur, 1.2 mm long; patella and tibia, 1.2 mm; metatarsus, 0.7 mm; tarsus, 0.5 mm. Second patella and tibia, 0.9 mm long; third, 0.7 mm; fourth, 1.1 mm.

Male. Coloration like female except that the abdominal patches are fused, forming a longitudinal band with wavy outlines. Eyes subequal in size. Anterior median eyes 1.2 diameters apart, 0.3 from laterals. Posterior median eyes 1.5 diameters apart, 1 diameter from laterals. Height of the clypeus is 2.5 diameters of the anterior median eyes. Total length 2.3 mm. Carapace 1.3 mm long, 1.0 mm wide. First femur, 2.2 mm long; patella and tibia, 2.5 mm; metatarsus, 2.0 mm; tarsus, 0.8 mm. Second patella and tibia, 1.7 mm long; third, 1.0 mm; fourth, 1.7 mm.

Distribution. It is probable that the southernmost records of *Anelosimus rupununi* belonged to this species. All were females and may have been misidentified.

BEHAVIOR

Observations were conducted from November, 1975, through January, 1976, (Period I), and from March through June, 1976, (Period II), in a citrus orchard located within the municipal limits of



Figs. 1-4. Anelosimus lorenzo new species. 1. Female, dorsal view without appendages. 2-3, Epigynum. 2. Dorsal view, cleared. 3. Ventral view. 4. Left male Palpus. Scale line: Fig. 1, 1.0 mm, Figs. 2-4, 0.1 mm.

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San Lorenzo, Paraguay, approximately 15 km east of Asuncion. Initial searches confirmed the presence of 5 colonies during Period I, with 12 additional smaller colonies found during Period II. A large colony of approximately 550 adults and juveniles, and 50 egg sacs, was collected and established in a 1 m³ screen cage on a potted *Coleus* plant within an entomological greenhouse. The following observations were made on both field and laboratory colonies.

Spinning behavior and webs. The 5 colonies observed during Period I ranged in estimated volumes of web enclosures from 0.3 m^3 to 1.4 m³. The 12 smaller colonies observed during Period II were much smaller, with the largest having ana estimated volume of 0.2 m^3 . The web periphery of all colonies was covered with loosely spun silk, while the interior consisted of densely spun silk platforms. Webs housing the colonies did not differ from the webs of *A. eximius* figured by Millot (1949) and Brach (1975), or from the webs of *A. rupununi* illustraded by Levi (1972). Additional webs of unspecified colonial species of *Anelosimus* are illustrated in Stejskal (1976).

The remains of many large insects, notably cerambycid, carabid and scarabaeid beetles, were observed throughout the web structure. Portions of the web of the larger colonies had apparently fallen into disuse, as these were cluttered with dead vegetation and insect parts, as described by Millot (1949). Dead or dying leaves in the interior of the communal web were curled and sheathed with silk to form retreats. Stejskal (1976), in a still unconfirmed report, contended that unspecified species of *Anelosimus* pierce the epidermis of the undersides of mango, citrus and coffee leaves and actively imbibe the cytoplasm, and further hypothesized that these species would not survive on other species of trees. More observations on the feeding behavior of these spiders are obviously needed to check the validity of these claims. The colony figured by Brach (1975) was not located in these plants. He observed no dead leaves, perhaps because spiders were not piercing and drinking from the leaves.

Citrus trees housing all 5 colonies during Period I were heavily attacked by mealybugs, *Pseudococcus* sp., which were tended by ants, *Crematogaster quadriformis vezenyii* Forel. The distribution of both mealybugs and ants reached the colonial web on the branches where the colonies were located. Many mealybugs, and a few ants, were found entangled at the branch-web interface. No abnormal fruit or leaf developments were noted within the communal web, with the exception of the dead and curled leaves serving as retreats. Stejskal

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(1976) concluded that colonial species of *Anelosimus* were more harmful than beneficial in Venezuelan orchards, where they are actively treated with pesticides.

Most web spinning and repair occurred at night. Webbing was spun as several spiders reinforced draglines from which they dispersed to spin subsequent peripheral silk or dense platform silk. This behavior was qualitatively the same as that found in *A. eximius* (Brach, 1975). Unlike *A. eximius* (Brach, 1975), *A. lorenzo* did not always found colonies at the extremities of leaves or branches. 3 of the 5 large colonies, and 7 of the 12 smaller colonies were located at positions intermediate between the twig or branch junction and its tip. This behavior is much like other species of *Anelosimus* (Stejskal, 1976).

Small colonies were always found in trees adjacent to large colonies, hinting that colony foundation is carried out by small groups of spiders, or sociotomy (Jackson and Joseph, 1973). All the small colonies observed appeared before the onset of cooler winter weather. The large size of colonies, both in populations and webbing, and conversations with local farmers, suggest that colonies are perennial. Stejskal (1976) observed repeated colony relocation over a 3 yr period, and attributed this activity to the dry microenvironment produced when the spiders' activities killed leaves.

Social interactions. In a rigorous analysis of social behavior in the Theridiidae, Kullmann (1968, 1972) ranked A. eximius (=Theridion eximius) at the pinacle of social evolution within this family. Wilson (1971) considered A. eximius to be quasisocial, due to the presence of members of the same generation in communally constructed and maintained webs, the existence of communal cooperation in prey capture, and the indiscriminate feeding of the juveniles. Brach (1977) emphasized the importance of cooperation between adults, or parasociality (Shear, 1970), in the evolution of social behavior in Anelosimus. That A. lorenzo parallels A. eximius at every level of behavior observed (Table 1), suggests that quasisociality is probably quite widespread within Anelosimus. A. rupununi, with extensive communal webs and populations in excess of 1,000, is also probably quasisocial, and as more observations are made on other species, this list will undoubtedly have to be increased. It is tempting to speculate that some reports on the social behavior of A: eximius may have inadvertently been of other species, especially due to the high degree of morphological similarity found within species groups.

TABLE 1

COMPARATIVE BEHAVIORAL AND ECOLOGICAL PARAMETERS OF THREE SPECIES OF *ANELOSIMUS*. DATA FOR *A. STUDIOSUS* AND *A. EXIMIUS* TAKEN FROM BRACH (1975, 1977). DATA FOR *A. LORENZO* FROM THIS STUDY. BEHAVIORS ARE DESCRIBED IN BRACH (1975, 1977).

PARAMETER	Anelosimus studiosus	Anelosimus eximius	Anelosimus lorenzo
Geographic range	Temperate- subtropical North America	Tropical South America	Subtropical southern South America
Colony populations	~50	>200	>200
Cooperative prey capture	present	present	present
Communal feeding	present in juveniles, not in adults	always present	always present
Reproductive females/colony	1	>I	>1
Cannibalism	present .	present	present
Brood feeding	discriminate	indiscriminate	indiscriminate
Dispersal	solitary gravid females	sociotomy?	sociotomy?
Colony life span	annual .	perennial	perennial
No. females/ No. males	~1.0	~20-79	~50
Species recognition	strong	weak	weak
Social level	subsocial	quasisocial	quasisocial

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Field colonies of A. lorenzo accepted spiders from other colonies without any overt sign of aggression. Other unidentified species of Theridiidae, when placed in webs, were ignored until they were apparently accidentally encountered by resident spiders, at which time they were attacked. Other behavioral observations (Table 1) were made much the same way as by Brach (1977), and will not be further elaborated. Nevertheless, Brach (1977) failed to comment on sex ratios. Although field data are few, it is apparent that the sex ratios of quasisocial Anelosimus are strongly skewed in favor of females. Brach (1975) speculated that the preponderance of females was the product of differential cannibalism on males, resulting in the female biased quarternary sex ratio. However, data are not available on primary and secondary sex ratios for these spiders to ascertain if cannibalism is a valid hypothesis. Whatever the cause, female dominated populations undoubtedly affect the population genetics of these species (Fisher, 1930), and one would expect that females are the mobile sex (Cannings and Cruz Orive, 1975), which would tend to indicate that inbreeding may be quite high.

The influence of sex ratio on the population genetics of these spiders becomes more evident when the mode of sex determination is considered. Although spiders are diploid, sex determination in the Araneae is characteristically through a complex system of multiple chromosomes, with males being heterogametic (White, 1973). Under normal conditions, brothers and sisters within a colony would share the same number of genes in common with one another through common descent. However, if the female homogametic chromosomes have significantly more active gene sites, then sisters would share more genes with one another through common descent, than do brothers. Thus, at the sex-linked loci, kin-selection (Hamilton, 1972) could contribute to the evolution of social behavior in the species of Anelosimus in a manner somewhat analogous to the assumed action in the Hymenoptera. Undoubtedly, if such a situation does indeed occur, morphological and behavioral modifications would to have evolved before sociality could be achieved, such as the loss of speciesspecific tactile recognition (Brach, 1977). If indeed quasisocial Anelosimus are highly inbred, the possibility that kin selection is important would be much more probable (Hamilton, 1972).

Sex ratios dominated strongly in favor of females may also inadvertently produce a reproductive division of labor, especially in light of the indiscriminate feeding of juveniles by adults. If there are

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not a sufficient number of males present in the colony to inseminate all reproductively receptive females, only inseminated females would produce viable young as thelytoky is unknown in spiders (White, 1973). Species of Anelosimus that are now considered to be quasisocial may thus be found to be functionally eusocial (sensu Wilson, 1971). However, there is still no evidence of an actual anatomical of physiological distinction among non-reproducing spiders that would qualify them as a true caste in the usual sense employed in the study of social insects.

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LITERATURE CITED

BRACH, V.

. . .

- 1975. The biology of the social spider Anelosimus eximius (Araneae: Theridiidae). Bull. So. Cal. Acad. Sci., 74: 37-41.
- 1977. Anelosimus studiosus (Araneae, Theridiidae) and the evolution of quasi-· sociality in Theridiid spiders. Evolution, 31: 154-161.

CANNINGS, C. & L. M. CRUZ ORIVE.

1975. On the adjustment of the sex ratio and the gregarious behavior of animal populations. J. theor. Biol., 55: 115-136.

FISHER, R. A.

1930. The genetical theory of natural selection. Clarendon, Oxford. 272 pp. HAMILTON, W. D.

1972. Altruism and related phenomena, mainly in social insects. Ann. Rev. Ecol. Syst., 3: 193-232.

KULLMANN, E.

- 1968. Soziale Phaenomene bei Spinnen. Ins. soc., 15: 289-298.
- Evolution of social behavior in spiders (Araneae: Eresidae and Theri-1972 diidae). Amer. Zool., 12: 419-426.

LEVI, H. W.

- 1956. The spider genera Neottiura and Anelosimus in America. Trans. Amer. Micros. Soc., 75: 407-421.
- 1963. The American spiders of the genus Anelosimus (Araneae, Theriidae). Trans. Amer. Micros. Soc., 82: 30-48
- 1972. Taxonomic-nomenclatural notes on misplaced Theridiid spiders (Araneae, Theridiidae), with observations on Anelosimus. Trans. Amer. Micros. Soc. 91: 533-538.

MILLOT, J.

Araignees sociales. In P. Grasse (ed.) Traité de Zoologie, 6: 979 pp. 1949. Masson, Paris.

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1976. Aranas sociales destructoras de las plantas de cafe, citricos y mangoes en Venezuela. Turrialba, **26:** 343-350.

WHITE, M. J. D.

1973. Animal cytology and evolution. 3rd Edition. 961 pp. University Press, Cambridge.

WILSON, E. O.

1971. The insect societies. 548 pp. Belknap Press-Harvard, Cambridge.

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